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Photoreception and the polyphyletic evolution of photoreceptors (with special reference to Mollusca)*

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Abstract: The general expression of the transcription factor gene *Pax-6* homologues and the overall presence of the photopigment opsin have cast doubt on the polyphyletic evolution of photoreceptors. Herein it is proposed that the evolutionary pathway of photoreceptors reflects two different, successive processes: (i) the (monophyletic?) differentiation of photoreception as such, mediated by a specific transcription factor gene (such as *Pax-6* or *sine oculis*) and (ii) the genetic information of that induction factor (normative unit for photoreception). The latter stimulates the (polyphyletic) differentiation of the photoreceptors themselves through its multiply convergent co-options with variable network-modifications (intercalation of different genes). The expression of transcription factor genes does not *per se* imply homology of the differentiated photoreceptors (but at most some pattern of homoiology). The differentiation of both receptor types, ciliary versus rhabdomeric, in one and the same cell during development (of veliger larvae; Blumer 1996) shows them to be interchangeable structures (mere morphs). Apparently dependent of functional requirements, the structural type of the receptive organelle has no direct bearing upon the homology identification of the photoreceptors. This obviates the need to propose separate (ciliary and rhabdomeric) precursor cells in metazoans. A possible primitive "dermal" receptive cell which was polyphyletically adapted for metazoan photoreceptors is discussed. The rich morphological diversity of photoreceptors (including the larval organs) in Mollusca appears to represent in-group differentiations. Their polyphyletic lines are surveyed and the fine structure of eyes of three pteriomorph Bivalvia species—*Lima lima* (Linnaeus, 1758) (with a subdivided retina), *Chlamys varia* (Linnaeus, 1758), and *Pseudamussium peslutre* (Linnaeus, 1771) (with incomplete proximal retina)—is reported.

Key words: eye evolution, morphogenesis of photoreceptors, photoreceptor structure, transcription factor gene *Pax-6*, *Lima* and *Pseudamussium* (Bivalvia)

Photoreceptors (photoreceptive cells) and more differentiated photoreceptive organs (ocelli, eyes) are crucial sensory equipment for environment information and for orientation and are, therefore, widely differentiated within the animal kingdom. Their morphologically diverse organization raises questions on evolutionary relationships. New knowledge provides new views, and these are discussed herein.

The pioneer in ultrastructure research on photoreceptors, R. Eakin (1963, 1965, 1968), advanced the hypothesis that the evolution of photoreceptors followed two phylogenetic lines: the first involved opsin-containing surface enlargements of the cilia or flagella membrane (ciliary type) and the second involved enlargements in the form of microvilli of the distal cell membrane (rhabdomeric type). Some photoreceptors, however, have cilia as well as microvilli (mixed type). In contrast, Salvini-Plawen and Mayr (1977) proposed a convergent, polyphyletic origin of photoreceptors in about 40-65 independent lines. Later, Salvini-Plawen (1982) refuted a restriction of the "rhabdomeric line" to the cerebral photoreceptors of Protostomia or Spiralia (Eakin 1979).

More recently, the widespread findings of the molecular prerequisites for photoreception have blurred the homology debate on photoreceptive organs with regard to monophyly versus polyphyly. Homology implies similar structures or characters that are based on the same singular (monophyletic) evolutionary origin. The debate refers, on the one hand, to the ubiquitous presence of the (homologous) photopigment opsin and, on the other hand, to the expression of transcription factor gene *paired-box 6* (*Pax-6*, Pax6) homologues and other genes in photoreceptive cells in Triploblastica. Molecular biologists rapidly postulated that all photoreceptive cells and organs (ocelli, eyes)—at least of Triploblastica—are monophyletically homologous (Gehring and Ikeo 1999, Gehring 2001, 2004, Arendt and Wittbrodt 2001, Arendt 2003). With respect to this new perspective, E. Mayr (2002: 226) concluded "The origin of eyes in 40 branches of the evolutionary tree was always considered to be an *independent* convergent development. Molecular biol-

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ogy has now shown that this is not *entirely* correct" [italics by the present author]. Subsequently Mayr explained (2002: 227) "When survival is favored by the acquisition of a new structure or other attribute, selection makes use of all available molecules already present in the genotype"—that also includes the multiple convergent co-option of a transcription factor gene for receptor cell differentiation (see below).

MONOPHYLETIC PHOTORECEPTORS IN TRIPLOBLASTICA?

According to Arendt and Wittbrodt (2001: 1546), the polyphyly of photoreceptors would be restricted to Protista, Cnidaria, many "aberrant" ("ectoptic/extraocular/extraretinal") organs (pygidial eyes in Polychaeta, pallial photoreceptors in Bivalvia, or neural ocelli in Acrania/Cephalochordata) and the cerebral photoreceptors in "Bilateria". The monophyly of cerebral eyes in Triploblastica (excluding the bilateral Cnidaria and Ctenophora; cf. Salvini-Plawen 1978) is based upon the general presence of opsin and the shared expression of and regulation by the transcription factor gene *Pax-6* (Gehring and Ikeo 1999, Gehring 2001, 2004, Arendt and Wittbrodt 2001, Arendt 2003). It is, however, very difficult to comprehend such a homology in structurally very different organizations. Examples include complex eyes in Arthropoda, the inverse eyes of Vertebrata, or the everse eyes in Cephalopoda. Closer examination leads to a proposed subdivision of the evolutionary pathway of photoreceptors to reflect two different processes. The first is the (monophyletic?) differentiation of photoreception (later controlled by opsin photopigments) and mediation by a transcription factor gene that induces receptor cell differentiation. The second is the multiple stimulation by that induction factor to differentiate (polyphyletic) photoreceptors through multiply convergent co-options with variable network-modifications (intercalation of different genes).

In a strict sense, genetic expression leads to clear homology of morphological structures or organs only when (in the simplest case) they correspond by inheritance one-to-one to a genomic locus or its orthologues (in other species). More generally, however, genes interact with each other to effect a specific developmental function and thus form a hierarchical, developmentally interactive, regulatory network (Fernald 2000, Davidson and Erwin 2006). Transcription factor genes act fairly dispersed within such a network, and the *Pax-6* expression is not specific for photoreception. It is also involved in morphogenesis (structural differentiation) of the cerebral center as well as in chemosensory organs. In squids, besides in the developing eye (but not in the retina) and cerebral tissues, *Pax-6* additionally expresses in the arms (suckers) and in the mantle (Tomarev *et al.* 1997, Hartmann *et al.* 2003). Moreover, *Pax-6* generally functions in a wide range of processes in further cells, including the interactions with other proteins (*e.g.*, Simpson and Price 2002). As underlined by Wagner (2007) with respect to the transcription factors, the regulatory network within which *Pax-6* expression in *Drosophila* is embedded includes the genes *eyeless*, *eyes absent*, *dachshund*, and *sine oculis*—this differs from the detailed network in vertebrates as exemplified by *Xenopus* (Fig. 1). Thus, although they include *Pax-6* or a homologue, the gene regulatory networks for the development of the insect and vertebrate eyes are derived independently (by intercalation of different genes); in morphological terms, this reflects homoiology at most (representing convergent structures derived from a homologous character). Therefore, *Pax-6* homologues expressing within different regulatory networks do not infer photoreceptor homology (see also Zuckerkandl 1994, Fernald 2000, Nielsen and Martinez 2003). Moreover, the *sine oculis* gene of *Drosophila* (and *optix* of vertebrates) clearly existed at the very base of the metazoans (Pichaud and Desplan 2002, Stierwald *et al.* 2004). Not the *Pax-6*, but the *sine oculis* gene (or a homologue of it) might be the important ancestral transcription factor gene for receptor differentiation (see also Pineda *et al.* 2002). In any case, only gene regulatory networks that include an almost identical combination of transcription factors (called 'character identity networks' by Wagner 2007) appear to execute specific developmental programs that reflect homologous structures and organs.

There is a fundamental difference between potentially monophyletic, primitive photoreception of cells based upon a particular gene regulatory network, and polyphyletically differentiated, distinct photoreceptors or organs (ocelli, eyes) incorporating independently modified gene regulatory networks (which in Triploblastica includes *Pax-6* homologues). This discrepancy, underlined 30 years ago by Salvini-Plawen and Mayr (1977: figs. 2, 9) for dermal light sense versus photoreceptors, is often neglected (*e.g.*, Vanfleteren 1982, Gehring 2004). Such prerequisite primitive cells with a transcription factor gene for receptor differentiation possibly still have "dermal" light sensitivity (sensitive cells without pigment; cf. Millott 1968). This would be similar to the case in Echinodermata (Yoshida and Takasu 1984), particularly in the echinoid *Paracentrotus* (Czerny and Busslinger 1995, cf. also Arendt and Wittbrodt 2001). It would also correspond to the general sensitivity involved in the shadow reflex ("off response") in many molluscs and especially of the pallial lobes in Bivalvia (Kennedy 1960, Mpitsos 1973, Messenger 1991, Morton 2001). The particular gene regulatory network of light-sensitive dermal cells became—by selection—the functionally successful, normative pattern or induction unit for photoreception. It was then repeatedly co-opted to

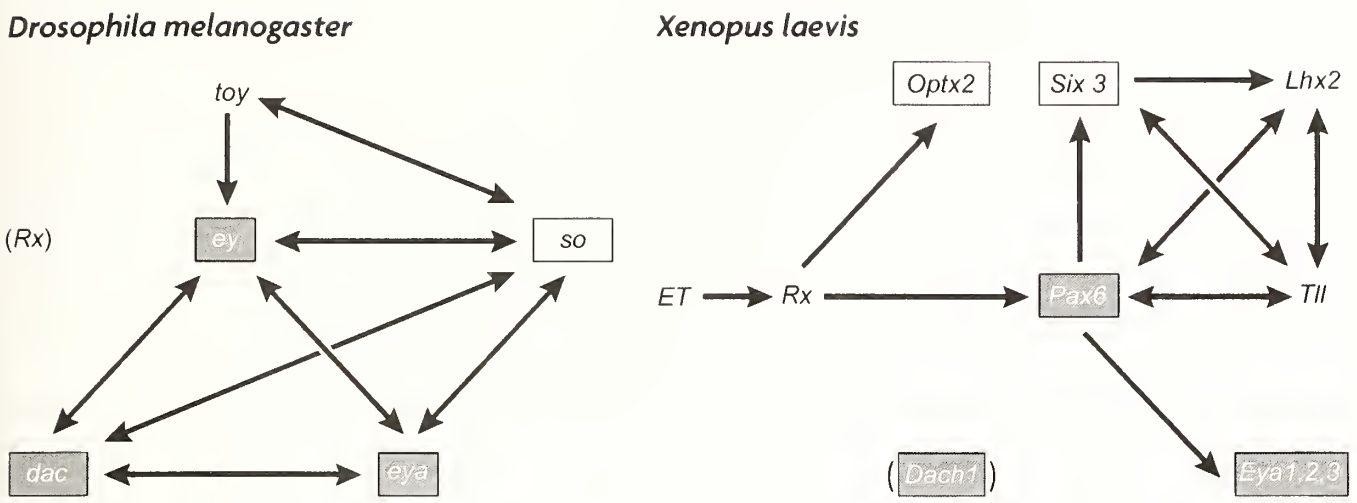

Figure 1. The non-homologous genetic regulatory networks for eye development in insects (*Drosophila*) and vertebrates (*Xenopus*); orthologous genes in grey boxes, paralogous genes in white boxes (after Wagner 2007). In *Drosophila*, the gene *twin of eyless* (toy) activates *eyeless* (ey) which is necessary for eye development; its network includes the genes *eyes absent* (eya), *dachshund* (dac), and another transcription factor *sine oculis* (so). In *Xenopus*, the gene *retinal homeobox* (Rx) is essential and regulates *paired-box 6* (Pax6, a homologue of *eyeless*) which includes in its network homologues of *eyes absent* (Eya1,2,3) as well as the *sine oculis homeobox* homologue 3 (Six 3) and its paralogue Optx2. A Rx homologue is also present in *Drosophila* but not involved in eye development. The non-homology of both networks is supported in vertebrates by Eya1,2,3 which do not regulate the *dachshund* homologue Dach1, as well as by additional genes involved.

serve as the foundation for the independent structural differentiation (morphogenesis) and evolution of photoreceptors. This initial normative induction unit, however, multiply modified its gene regulatory network by intercalation of different genes (see also Gehring and Ikeo 1999, Gehring 2001, 2002), yielding the variously differentiated, polyphyletic photoreceptors and organs (see Wagner 2007). The expression of certain specific factors such as *Pax-6* of the (otherwise not identical) network has been mistaken for homology of the photoreceptors themselves. As outlined elsewhere (Salvini-Plawen 1998a: 139), gene expressions appear to reflect normative regulators only and do not imply homology of the induced structures. Moreover, the hypothesis by Arendt and Wittbrodt (2001) of a homology of cerebral photoreceptors throughout all "major bilaterian branches" suffers from subjectivity: it claims discrepancies to be secondary losses and disregards more precise homology criteria.

Molecular biologists often are not necessarily aware of the synchronously differentiated organ systems within the complex "bauplans". First, the two nervous systems (including sense organs) of Triploblastica—gastroneural (at least in Spiralia) versus epineural—are not homologous and may simultaneously be present (Salvini-Plawen 2000). Second, it is functionally consistent that the photoreceptors of directedly moving organisms ("bilaterians") became differentiated by selection pressure (stimulation) at the anterior body and connected to the cerebral ganglia. This condition parallels the "pygidial" photoreceptors in several retrograde-moving Polychaeta-Sabellidae (Purschke *et al.* 2006) as well as the photoreceptors at the exposed mantle edge in Bivalvia (see below). Such conditions, however, reflect a general selection pressure towards convergent formation. Restricted solutions based on physical laws also play a role (Fernald 2006). Location *per se* is not proof for homology—unless other criteria also provide evidence. Such criteria include relationship, continuity, structural and/or developmental intermediates, and an identical gene regulatory network.

Thus, the present analysis focuses not on the origin of initial light sensitivity (which might be monophyletic) or the differentiation of photoreception as such. Rather it deals with the multiply stimulated "subsequent divergent, parallel and convergent evolution" of photoreceptors (Gehring 2004: 707 which in fact represents polyphyly). It involves independently modified and co-opted gene regulatory networks in which different genes are intercalated (see also Gehring and Ikeo 1999, Gehring 2001, 2002). This process leads to the convergent, selectively adapted, polyphyletic photoreceptor cells and organs (ocelli, eyes). Regulator genes are merely competent for the transcription towards photoreceptive cell differentiation but not for the adaptively convergent-stimulated, structural differentiation of the multiple cerebral and "ectoptic/extraocular/extraretinal" photoreceptors themselves.

PHOTORECEPTIVE MEMBRANE ENLARGEMENTS

With respect to the distribution of the two different types of photoreceptive membrane enlargements, a phylogenetically inherited occurrence can be attributed only to a taxon level ranging between phylum and order (Vanfleteren and Coomans 1976, Salvini-Plawen and Mayr 1977). This thoroughly contradicts the separation of photoreceptor evolution into a protostome (rhabdomeric) and a deuterostome (ciliary) line (Eakin 1963, 1965, 1968).

In addition to the ciliary and rhabdomeric receptor types, a third type called "diverticular" was recognized (Salvini-Plawen and Mayr 1977, Salvini-Plawen 1982). It originates from non-epidermal (sunken, ganglionic), aciliary cells (neurons) which have an unpleated receptor surface or show some diverticular membrane enlargements. An example is the ganglionic pigment-cup ocelli (Hesse cells) in the neural tube of *Branchiostoma*; they lack both cilia and microvilli. Such cells secondarily differentiated their cell membrane to represent surface-enlarging diverticulae. Without knowledge of their genesis, they can easily be confused with the rhabdomeric type (Salvini-Plawen 1982). Although later authors (Ruiz and Anadon 1991) claimed that this type was likewise rhabdomeric, *Pax-6* is not expressed in these Hesse cells (Glardon *et al.* 1998). Accordingly, dermal receptor cell differentiation by that induction factor (normative unit) is not involved. The seemingly exceptional condition in *Salpa*—with neurally derived, aciliary receptor cells with their hyperpolarizing "off-response" (Gorman *et al.* 1971; see below)—coincides with the diverticular receptor type (Salvini-Plawen 1982). This is also valid for the hyperpolarizing response of two photosensitive neurons of the abdominal ganglion in *Aplysia* Linnaeus, 1767 (Krauhs *et al.* 1979, Andresen and Brown 1982; see below). They also lack cilia and microvilli (diverticular type).

In view of such a condition, one of the pressing questions is why photoreception involves, on the one hand, ciliary and, on the other hand, microvillar (rhabdomeric, diverticular) membrane enlargements. Muñoz-Cuevas (1975) as well as Vanfleteren and Coomans (1976) presented an induction theory with a ciliary structure as an organizer (contradicted by Salvini-Plawen 1982 and Yamamoto 1985). Eakin (1979) advanced a concept based on mutations (discussed and contradicted by Salvini-Plawen 1982). Both hypotheses are inconsistent. In fact, most ciliary type receptors represent phylogenetically young organs (Vanfleteren and Coomans 1976, Salvini-Plawen and Mayr 1977, Burr 1984). Based on structural organization, ciliary reception has apparently changed to rhabdomeric reception in certain cases. These considerations point to ciliary differentiation as the initial (and/or original) type. This led Salvini-Plawen to propose a functional dependence and to conclude (1982: 151) that "the polyphyletic diversity of photoreceptors appears to be due to different functional requirements at different times during radiation of evolutionary lines."

Although functional correlations are still poorly understood, several investigations support such a principal dependence. Some earlier findings in Platyhelminthes-Polycladida (Ruppert 1978, Eakin and Brandenburger 1981, Lanfranchi *et al.* 1981) of ciliary receptors in larvae (adult photoreceptors are rhabdomeric) advanced the idea of potential structural change according to different functional requirements in larvae and adults.

In Gastropoda, the veliger larvae (but not others, see below) possess photoreceptors. They represent the organs of the adult organization precociously advanced into the larval stage (acceleration; Salvini-Plawen 1980b and below). The ocelli or eyes of adult gastropods typically show a rhabdomeric receptor structure (summarized in Blumer 1996); some species, however, have ciliated and microvillous receptors (mixed type; see below). Because of acceleration, a rhabdomeric receptor structure should also be present in the larval ocelli. This indeed is the case in short-term or actaeplanic veligers (Hughes 1969, Chia and Koss 1978), whose rhabdomeric photoreceptors might be sufficient for the short stay in the water column. Based on the argument that the photoreceptive demands in larvae with a long pelagic life (long-term or teleplanic larvae) will change accordingly, we might expect the receptive structure to change. Besides the evidence in Platyhelminthes-Polycladida (above), the finding of ciliary photoreceptive structures in the long-term veliger larva of *Ilyanassa obsoleta* (Say, 1822) (Crowther and Bonar 1980) supported this point of view.

In accordance with this hypothesis (Salvini-Plawen 1982, 1988), the photoreceptive structures in long-term (teleplanic) veligers were then demonstrated to correlate with the ciliary type (Blumer 1994, 1995, 1998, 1999). Moreover, the investigations by Dilly (1969) on *Pterotrachea mutica* (Lesueur and Peron, 1817), and by Blumer (1999) on *Atlanta peroni* Lesueur, 1817, revealed that a permanent pelagic life without a benthic phase (such as in Gastropoda-Heteropoda) might also be correlated with ciliary photoreceptors, even if variously adapted. Other heteropods, such as *Carinaria* Lamarck, 1801, however, still differentiate close to metamorphosis a photoreceptive segment of presumed rhabdomeric type. Structurally, this represents a mixed type (Blumer 1998) with a dual function. Thus, short-term (actaeplanic) larvae that spend less than six weeks in the plankton (Scheltema 1989) are correlated with rhabdomeric receptors whereas long-term pelagic life (larvae/adults) functionally correlates with ciliary receptors. Finally, Blumer (1996) demonstrated for teleplanic veliger larvae that the photoreceptive part of sensory cells themselves is successively altered during the life cycle: microvilli (for rhabdo-

meric structure) as well as photoreceptive cilia (monociliary to polyciliary) are added.

These conditions support the idea (Salvini-Plawen 1982) that the ciliary photoreceptive structure is adaptive for a pelagic existence, *i.e.*, is due to the functional requirements for this environment. This may refer to the reception of different wavelengths or to the sensitivity. Mobile benthic life no doubt demands that photoreceptive organs sense for orientation and/or vision (correlated to rhabdomeric structure?). In contrast, larvae within the water column need information on the direction of the light (correlated to ciliary structure?) for optimal feeding close to the surface and thus for the diurnal migration to that layer (periodicity). In sessile or semi-sessile animals, photoreceptors must recognize light/shadow (antipredatory) conditions with a hyperpolarizing "off-response" of (ciliary) receptor potential (cf. also "dermal" light sensitivity). Accordingly, this is apparently correlated with detecting changes in light intensity (decrease or light/shadow reactions) in very slow moving or sessile animals, with color changes including dorsal/ventral reactions and paling response in pelagic organisms, and with rhythmic behavior like diurnal migration of plankton and/or circadian rhythms (Land 1968, 1984, Salvini-Plawen 1982, 1988). In vertebrates, this appears to be performed by the dorsal (pineal and parietal) eyes, in direct inheritance of the (originally paired) ocellus in larvae of Tunicata-Ascidiacea (Hamasaki and Eder 1977, Salvini-Plawen and Mayr 1977). A long-term filter-feeding nourishment—during which the perception of light direction was sufficient—may explain why the ciliary receptor type was genetically firmly anchored. Then, when the shift to a directed food uptake stimulated the differentiation of new, repetitively (iteratively) homologous lateral eyes, this receptor type was retained (*i.e.*, not changed to the rhabdomeric morph). Rhabdomeric photoreceptive organs, however, may be called upon to correlate yes/no registrations of light stimuli with a depolarizing "on-response" (existence and/or increase of light intensity and direction); this would be more favorable for orientation.

HOMOLOGY AND THE PRECURSOR CELL STRUCTURE

Results with veliger larvae (Blumer 1996) show that one and the same photoreceptive epidermal cell can change its receptive surface structure according to function. This implies that photoreceptive structure has no direct bearing upon the identification of homology of the photoreceptive organs. A case in point is the Gastropoda. The same also holds true for Placophora, in which the monophyletic aesthetes and shell-eyes are ciliary and rhabdomeric structures. These structures are interchangeable and thus merely functionally conditioned different morphs. In other animal groups, however, the conditions appear to be different. In Sipunculida, for example, the inverse cerebral ocelli in the teleplanic larvae are not continuous with the adult everse cerebral tubes (Salvini-Plawen and Mayr 1977); the larval ocelli possess rhabdomeric receptive cells and appear to be homologous to the inverse pigment cup ocelli with rhabdomeric structure in polychaete larvae (Blumer 1997; not considered by Arendt and Wittbrodt 2001). Similarly, many members of Polychaeta have different organs for photoreception during their life cycle (Purschke *et al.* 2006): the larval ocelli may be retained as adult cerebral photoreceptors but more usually are replaced by adult cerebral organs (*e.g.*, Eakin and Westfall 1964, Rhode 1993). In late larvae, therefore, both pairs of photoreceptive organs may be visible (*e.g.*, in nectochaeta larvae of *Polydora* sp. (Spionidae) with outer larval and inner adult ocelli; pers. obs.). Only some of the pigmented or unpigmented larval ocelli investigated so far possess ciliary receptors. The altered photoreception requirements of larval and adult polychaetes, however, are reflected in the usual discontinuous differentiation of separate, non-homologous organs (versus/in contrast to Bartolomaeus 1992). The general predominance of rhabdomeric structure points to well-established adaptation (directed movement: cerebral photoreceptors) and, hence, to strong genetic anchorage. In contrast, ciliar structure appears to be the initial adaptive answer to photoreceptive requirements (*e.g.*, light-shadow reaction), with the rhabdomeric structure as a subsequent differentiation. The ciliary type is, thus, more frequently (still) represented in phylogenetically relatively young organs (Vanfleteren and Coomans 1976, Salvini-Plawen and Mayr 1977, Burr 1984). Such "new" requirements are evident in the teleplanic veliger larvae versus the "old" photoreceptors in adult gastropods.

This casts a new perspective on the homology criteria as related to photoreceptors. The results from long-term veligers considerably decrease the value of "compositional correspondence" of Remane's (1952) three principal homology criteria (positional correspondence, compositional correspondence, structural, and/or developmental intermediates). The ability to replace the receptive structure deletes one prominent morphological character for detailed homology comparison. Moreover, "positional correspondence" is also of limited value, as outlined above for cerebral photoreceptors. This diminishes the possibility to recognize convergences or parallelisms, unless there is different innervation or gene expression. At the same time, this contradicts the arguments of Arendt and Wittbrodt (2001: figs. 8(c), 9) and Arendt (2003) for separate precursor cells (ciliary versus rhabdomeric with opsin orthologues) in "Bilateria": one and the same cell can alter its photoreceptive part from a ciliary

to a rhabdomeric type (Blumer 1996). Thus, the precursor cells (*e.g.*, "dermal" light sensibility) probably corresponded to a neutral, "mixed" or combined type with cilium and microvilli (Arendt and Wittbrodt 2001: fig. 8(b)). This condition was already proposed by Salvini-Plawen and Mayr (1977: figs. 2, 9) and is supported by recapitulation in cephalopods (Yamamoto 1985).

Gehring's (2001, 2004) two-cell model of a sensory and a pigment cell as the original condition in metazoans is no longer realistic: two types of sensory cells are present. The first are so-called phaosome photoreceptors, which are single cells with an invaginated vacuole housing the receptive organelles (*e.g.*, Clément and Wurdak 1984, Purschke 2003) which generally show no shading pigment. The second are receptor cells with intracellular pigment. Although verified in only in a few photoreceptors, a sensory cell with cilium + microvilli + intracellular pigment probably represents an early photoreceptive cell associated with shading pigment. In gastropods, pigmented sensory cells are differentiated in conservative groups, such as in *Patella* Linnaeus, 1758 (Docoglossa; Hesse 1902, Marshall and Hodgson 1990) and in *Haliotis* Linnaeus, 1758 (Vetigastropoda; Hesse 1902, Tonosaki 1967, Kataoka and Yamamoto 1981). They are also present in several other representatives (*e.g.*, *Ilyanassa* Stimpson 1865, *Murex* Linnaeus, 1758, *Aplysia*, *Pleurobranchus* Cuvier, 1804; Hesse 1902, Hughes 1969, Gibson 1984). Photoreceptive cells with pigment granules are likewise present in the veliger larvae of *Smaragdia* Issel, 1869 and *Strombus* Linnaeus, 1758, in *Octopus* Cuvier, 1798, and other cephalopods as well as in additional animal groups (Eakin 1972, Yamamoto 1985, Blumer 1995).

Going further back in evolution, the Cnidaria clearly point to a single cell type with a mixed/combined or a ciliary receptor (with opsin) as being the primary precursor structure for photoreception. Although they lack a cerebral center, Cnidaria possess an astonishing range of various "ectoptic/extraocular/ extraretinal" photoreceptors (Salvini-Plawen and Mayr 1977), albeit without *Pax-6* expression (Sun *et al.* 2001). They are generally of the ciliary type, though microvilli may also be present (*e.g.*, Singla 1974, Singla and Weber 1982, Blumer *et al.* 1995, Nordström *et al.* 2003). Accordingly, the type of opsins appears to be more closely related to that of the ciliary receptors or c-opsins (Plachetzki *et al.* 2007, Suga *et al.* 2008). In *Leuckartiara* (Anthomedusae) the sensory cells with microvilli, combined with an unmodified cilium (Singla 1974), correspond fairly well to the precursor cells (*e.g.*, "dermal" light sensibility) proposed by Salvini-Plawen and Mayr (1977: figs. 2, 9). Also, the receptor cells in the scyphozoan *Cassiopea* as well as in the cubozoans *Tamoya* and *Tripedalia* are pigmented (Bouillon and Nielsen 1974, Yamasu and Yoshida 1976, Laska and Hündgen 1982). All these presumed structural prerequisites (cilium, microvilli, and pigment granules) may also be combined within one cell. An example is the photoreceptive cell of cubozoan planula larvae (Nordström *et al.* 2003). It has no neural connection to any other cells and is structurally intermediate between a photosensitive dermal cell and a primitive organ.

The presumed light-sensitive cells in certain sponge larvae (parenchymulae of *Amphimedon queenslandica*, formerly *Reneira*; Porifera-Haplosclerida) each possess a long cilium and are pigmented. Though neither neurons nor opsins are present (Plachetzki *et al.* 2007, Suga *et al.* 2008), they react to changes in light intensity (Leys and Degnan 2001).

Thus, the primitive condition is reflected by a single precursor cell type (also Arendt *et al.* 2004). As already proposed (Salvini-Plawen and Mayr 1977), cells with a cilium and with some microvilli (mixed type) probably represent the basic type for (dermal) photoreception in Metazoa. This basic type is then convergent-adaptively modified for morphogenesis. Opsins are lacking in poriferans. This supports the morphological classification of the sponges as Parazoa as opposed to the Histozoa or Gastrozoa (Salvini-Plawen 1978, 1998b). It also reflects the presence of non-opsin controlled ("dermal") photoreception in Metazoa. Accordingly, photoreception evolved independently of and prior to the differentiation of opsin photopigment. Later, an opsin-like protein arose as a visual pigment in basal Histozoa/Gastrozoa (see also Plachetzki *et al.* 2007). Due to functional demands/ adaptive "needs", opsin paralogues (by gene duplication) were differentiated within the same cells (see Blumer 1994). A correspondingly adapted opsin type became incorporated into the membranes of cilia. In the case of mixed receptors, a paralogue with a different type of transduction cascades additionally became incorporated into the microvilli (see also Arendt *et al.* 2004, Fernald 2006). This implies that two or more opsin paralogues can be differentiated within the receptive cells and would explain the expression of the "wrong" opsin in cells without respective membrane enlargements (Kumbalasiri and Provencio 2005). Over time, the cells were provided with intracellular pigment or associated with pigment cells.

The photoreceptive organelles in different flagellate Protista (Gehring 2001, 2004), however, appear to represent one or several alternative structural answers to the selective profit of photosensitivity. The most probable ancestors of Metazoa (based on their primitive monociliar/flagellate collar cells; cf. Rieger 1976) are the Choanoflagellata or Craspedomonadina (Salvini-Plawen 1978). They lack photoreceptive organelles or opsin genes (Plachetzki *et al.* 2007, Suga *et al.* 2008). Therefore, the phylogenetic-structural gap between photoreceptive protists and metazoans additionally points to sepa-

rate structural formations (morphogeneses) of the photoreceptive equipment. In contrast, the differentiation of photoreception itself, if monophyletic, distinctly points to an earlier process (see above).

POLYPHYLETIC PHOTORECEPTORS IN MOLLUSCA

Our current understanding of the general polyphyletic structural formation and evolution of photoreceptors remains unchanged: the evolutionary pathway of photoreceptors still reflects two different, successive processes. The recognition that the ciliary and rhabdomeric photoreceptive structures are interchangeable morphs, however, alters the premises for detailed homology comparison. Turning to Mollusca, how often within the phylum was such a transcription factor (as a normative induction unit for photoreceptive cell differentiation) convergently co-opted for structural formation (morphogenesis) of photoreceptors?

The wide range of life-styles in molluscs is reflected in a considerable variety of photoreceptive differentiations, from dermal light sensitivity to a rich diversity of ocelli and eyes (Messenger 1991). Larval and/or adult photoreceptors are present in several clades of Testaria (Placophora and Conchifera; cf. Salvini-Plawen 2006). On one hand, there are cerebrally innervated organs, restricted to larvae and organisms with a free head (Gastropoda, Cephalopoda). On the other hand, there are quite a number of "extraocular/ectoptic/extraretinal" organs. In Bivalvia, these are represented by a rich morphological diversity. Following the probable evolutionary history of molluscs (Salvini-Plawen 1990, 2006, Salvini-Plawen and Steiner 1996, Haszprunar 2000), however, they originally lacked any photoreceptors (see Solenogastres, Caudofoveata, Tryblidia, Scaphopoda; cf. Salvini-Plawen 1972, 1980b, 1982, Salvini-Plawen and Mayr 1977). Nonetheless, scaphopods do show dermal sensitivity with shadow responses (see Messenger 1991). Thus, all photoreceptive organs of different lines, including larval ocelli, appear to represent ingroup acquisitions, and no reliable descendance from differentiations in other spiralians can be ascertained.

Larval photoreceptors

Mollusc larvae primarily possess no photoreceptors (Salvini-Plawen 1980b, 1982, in contrast to Bartolomaeus 1992): no ocelli are differentiated in the larvae of Solenogastres, Caudofoveata, Scaphopoda, and protobranch as well as true lamellibranch Bivalvia. The pseudo-trochophoran larvae of Placophora, however, have a pair of ocelli which may persist for some time in the juveniles. Yet, these are post-trochal and laterally innervated (without a homologous equivalent throughout metazoans; Salvini-Plawen 1982, 1988). They have a mixed receptor type of microvilli and of cilia with a somewhat irregular membrane and "a few short microvilli-like projections" (Fischer 1980: 54; see also Rosen *et al.* 1979, Bartolomaeus 1992).

In contrast, the larval ocelli in Bivalvia-Pteriomorpha are cerebrally innervated and may persist in the adults at the first branchial filament. Therefore, a homology had been argued with the cerebral photoreceptors in gastropod veligers (Rosen *et al.* 1978, Bartolomaeus 1992). Four facts contradict this. (1) The most conservative Bivalvia-"Protobranchia" as well as the true lamellibranch bivalves lack ocelli, as mentioned above. (2) Within the Bivalvia (see Fig. 2), larval ocelli are thus restricted to several families of Pteriomorpha (Arcidae to Ostreidae; Pelseneer 1908, Hickman and Gruffydd 1971, Rosen *et al.* 1978, Morton 2001). (3) The larval gastropod photoreceptors are precocious (accelerated) adult organs, not yet differentiated either in the larvae of basal gastropods or in the plesiomorphically common organization of bivalves and gastropods. (4) The Bivalvia, whose pre-pedal body is still covered by the shell, clearly evolved prior to the separation of the free "head" (to which cerebral eyes are correlated). In the latter organizations—the Gastropoda and Cephalopoda—the shell is restricted to the pallio-visceral body. Consequently, a common precursor with "head" and cerebral photoreceptors in Bivalvia (and thereafter accelerated into the larvae) can be excluded (see "Protobranchia"). Accordingly, those larval ocelli have independently evolved only in Pteriomorpha (Pelseneer 1908, Salvini-Plawen 1982). This reflects an apomorphy for this clade (see Fig. 2). The sensory cells of these cup-like ocelli show a microvillous receptor structure with a cilium (Rosen *et al.* 1978), and in *Mytilus edulis* Linnaeus, 1758 larvae they react photo-positively (Bayne 1964).

Among the Gastropoda, the lecithotrophic pseudotrochophores of the most conservative clade, the stereoglossate Docoglossa (patellogastropods), lack photoreceptors. This is also true for pseudo-trochophores of several Vetigastropoda (*Haliotis*, *Fissurella* Bruguière, 1789) although these later ("pre-veliger"), however, develop photoreceptors, as do most true veligers of advanced gastropods. They represent the precociously advanced (accelerated) organs of the adult organization (Salvini-Plawen 1980b) rather than primary larval organs (Bartolomaeus 1992). The trend to accelerate the organs is obvious in *Haliotis* for example (Crofts 1937, Buckland-Nicks *et al.* 2002), and reflects the prolongation of larval life in the pelagic realm (differentiation of the prototroch to a velum with a second ciliated band, not homologous to a metatroch; Henry *et al.* 2007). In short-term veligers, the photoreceptors are rhabdomeric as in their adults. In long-term (teleplanic) veligers, however, the receptor structure is ciliary and changes during metamorphosis to a rhabdomeric or mixed type (Blumer 1994, 1995, 1996).

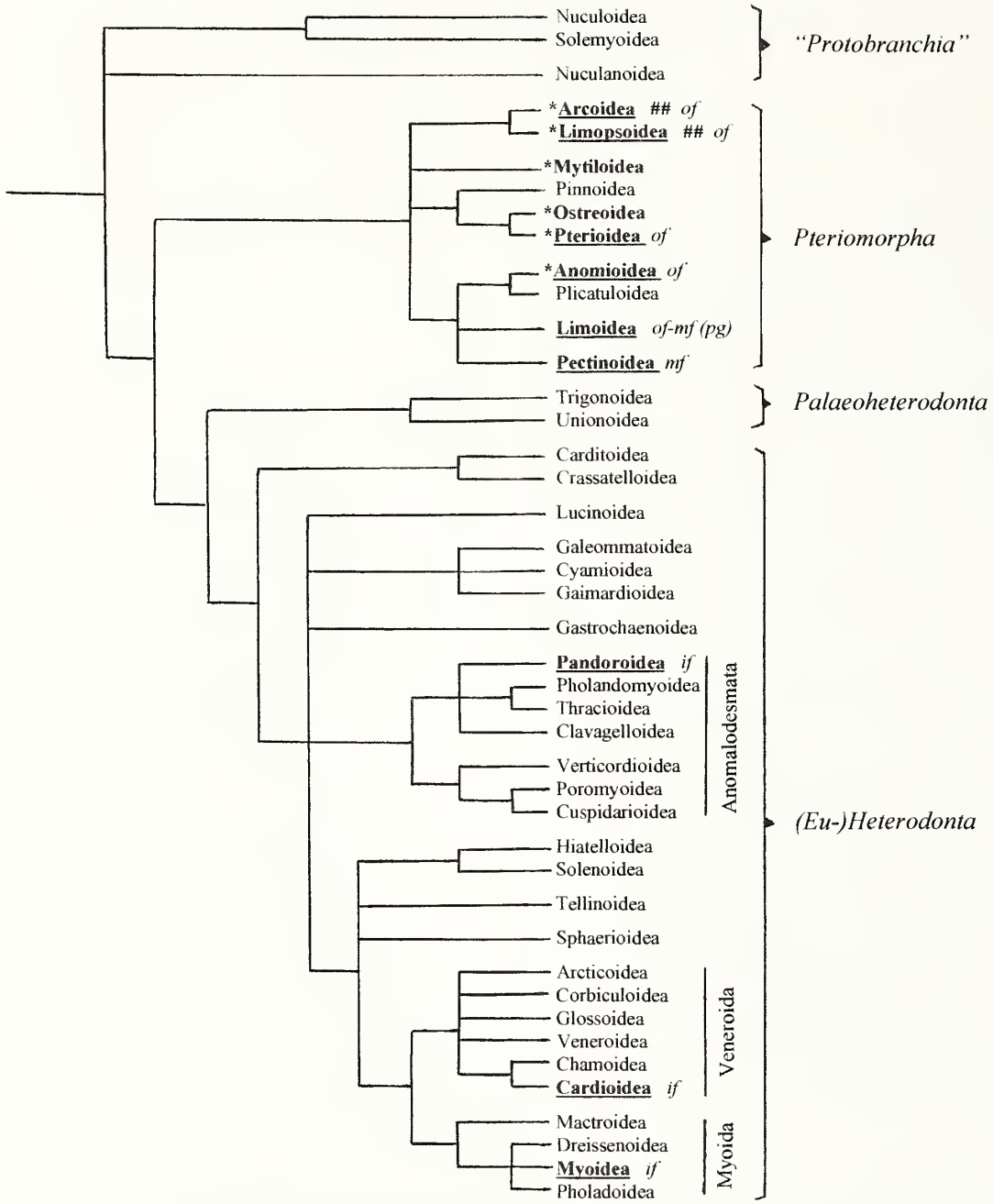

Figure 2. Tentative relationships of family groups within Bivalvia (after Steiner and Hammer 2000, Morton 2001, Giribet and Distel 2003), showing differentiation of photoereceptors. **bold**, with photoreceptors; underlined, with pallial photoreceptors; *, with larval/cerebral ocelli; # #, with compound eyes; *if*, at inner mantle fold; *mf*, at middle mantle fold; *of*, at outer mantle fold; *pg*, in periostracum groove (*of-mf*).

Organs in adults

Adult Mollusca differentiate several types of photoreceptive organs. Most exceptional are the aesthetes and shell-eyes in Placophora, but most prominent are the cerebral photoreceptors and eyes in Gastropoda and Cephalopoda. In autobranch Bivalvia (bivalves except for Protobranchia), different types of photoreoreceptors are present at the exposed mantle edge, the latter which serves for general orientation. Such non-cerebral photoreceptive organs are also known in gastropods and cephalopods (see Table 1).

Placophora

Adult Placophora possess a particular type of organ, the aesthete. These are laterally innervated and located dorsally, embedded within the secondarily calcified outer layer (tegmentum) of the eight shell-valves. In addition to other cell types, they include photoreceptors, which in some taxa have also given rise to advanced shell-eyes. The photoreceptive cells of the aesthetes are generally microvillous (rhabdomeric; Fischer 1988). In *Acanthochiton fascicularis* (Linnaeus, 1767), however, the aesthetes of the lateral fields of the valves differ by including sense cells with ciliary lamellate receptors (Fischer 1979). The shell-eyes (with lenses) also possess rhabdomeric receptor structures, whereas their marginal cells have ciliary receptors (Boyle 1969). In both these cases, the different receptors probably perform dissimilar functions (*e.g.*, for polarized light?). The extraordinary sensory organs within the valves of *Cryptoplax mystica* Iredale and Hull, 1905 (see Currie 1992) should also be mentioned although their function is still uncertain. They are surrounded by pigmented tissue and demonstrate a highly aberrant structure consistent with a photoreceptive and/or a balance organ.

Gastropoda

Cerebral photoreceptors in Gastropoda are everse but differentiated in various degrees. The structures range from open eye-pits such as in Patellidae (Docoglossa) or in Neritilidae (Neritopsina; Kano and Kase 2002) to the well-equipped lens-eyes in higher Caenogastropoda and Euthyneura (Salvini-Plawen and Mayr 1977). The receptor structure is generally rhabdomeric. Some species, however, show a mixed rhabdomeric and ciliary type: *Haliotis (Nordotis) discus* Reeve, 1846, *Viviparus viviparus* (Linnaeus, 1758), *Lacuna vincta* (Montagu, 1803) [=*Lacuna divaricata* (Fabricius, 1780)], possibly *Fartulum orcutti* (Dall, 1885), *Aporrhais pespelicani* (Linnaeus, 1758), *Aplysia punctata* (Cuvier, 1803) (see Howard and Martin 1984, Bartolomaeus 1992, Blumer 1995, 1996, Zhukov *et al.* 2006). In the ho-

Table 1. Polyphyletic evolution of photoreceptors, ocelli, and eyes in Mollusca (13 lines).

Taxon	Photoreceptors	Structure	Reference (see also text)
Solenogastres	—		Salvini-Plawen 1982
Caudofoveata	—		Salvini-Plawen 1982
(1) Placophora (larvae)	laterally innervated larval ocelli	mixed	Fischer 1980, Bartolomaeus 1992
(2) Placophora (adult)	aesthetes in general	rhabdomeric	Fischer 1988
Placophora (adult)	*Acanthochiton* lateral aesthetes	ciliary	Fischer 1979
Placophora (adult)	extrapigmental shell-eyes	rhabomeric	Boyle 1969
Placophora (adult)	shell-eye marginal cells	ciliary	Boyle 1969
Tryblidia	—		Salvini-Plawen 1982
(3) Gastropoda in general, adult	cerebral photoreceptors	rhabdomeric or mixed	Blumer 1996
Gastropoda-Heteropoda,	adult cerebral eyes	ciliary or mixed	Blumer 1999
Gastropoda, telephanic veligers	cerebral photoreceptors	ciliary	Blumer 1996
(4) Caenogastropoda: *Cerithidea*	pallial eye	ciliary	Rogge 1987
(5) Gastropoda-Anaspidea: *Aplysia*	abdominal neurons	diverticular	Messenger 1991
(6) Gastropoda-Onchidiidae	dorsal eyes	ciliary	Katagiri *et al.* 1985
Gastropoda-Onchidiidae	lens cells of dorsal eyes	rhabdomeric	Katagiri *et al.* 1985
(3?) Siphonopoda (cephalopods)	cerebral photoreceptors	rhabdomeric	Messenger 1991
(7) Siphonopoda	photosensitive vesicles	rhabdomeric	Messenger 1991
Scaphopoda	—		Messenger 1991
(8) Bivalvia-Pteriomorpha	cerebral/larval ocelli	rhabdomeric	Rosen et al. 1978
(9) Bivalvia-Arcoida	compound eyes at mantle edge	ciliary	Nilsson 1994
(10) Bivalvia-Arcoida	pigment-cup ocelli at mantle edge	rhabdomeric	Nilsson 1994
Bivalvia-Limoidea	eyes at mantle edge	mixed	Steiner 2001
Bivalvia-Pectinoidea	eyes with two retinae at mantle edge	rhabdomeric (proximal) ciliary (distal)	Steiner 2001
(11) Bivalvia-Pandoroidea	eyes with one or two retinae at siphons	both retinae ciliary	Adal & Morton 1973, Prezant 1984
(12) Bivalvia-Cardioidea	eyes at siphons	ciliary or mixed	Salvini-Plawen 1982
(13) Bivalvia-Myidae	phaosomes embedded in siphons	?rhabdomeric?	Light 1930

lopelagic Heteropoda, the retina of some species is subdivided in adults into an anterior segment with rhabdomeric receptor cells and a posterior segment with ciliary structure. Other heteropod species exclusively exhibit a ciliary type of cerebral photoreceptor, as do all heteropod veligers (Blumer 1998, 1999).

Apart from these cerebral organs, there is a clearly non-homologous pallial eye in the caenogastropod *Cerithidea scalariformis* Say, 1825. This has ciliary retinal cells that allow light/shadow reactions (Rogge 1987).

The photosensitive neurons in the abdominal ganglion in *Aplysia californica* J. G. Cooper, 1863 also deserve mention (see Messenger 1991). They consist of two receptor cells of the diverticular type (see above) which respond to light by hyperpolarization; each possesses intracellular organelles (lipochondria) with two orange-red photopigments (Andresen and Brown 1982).

The Onchidiidae—a family of the Gymnomorpha (within Aeropneusta the sister-group to Eupulmonata)—are also noteworthy. Several members possess, apart from cerebral eyes (stalked, rhabdomeric), dorsal papillae with up to seven eyes. These dorsal mantle eyes show an inverse retina as well as two lenses above each other (Stantschinsky 1908) and are pleurally innervated via pallial nerves. The fine structure reveals particular features: in *Onchidium verruculatum* Cuvier, 1830, the retina consists of cells with ciliary receptors which hyperpolarize with an "off-response" (Katagiri *et al.* 1985). The upper, unicellular lens is also photoreceptive but with a dense brush of microvilli (rhabdomeric type) and depolarizes with "on-response". In addition, *Onchidium* possesses single dermal photoreceptive cells, isolated or in small clusters, devoid of associated pigment; they have dense microvilli (rhabdomeric type) and depolarize with an "on-response".

Cephalopoda

The typically everse cerebral eyes of Cephalopoda initially differentiate a rudiment of the retina whose cells have a root-less cilium and microvilli. This subsequently develops into a rhabdomeric receptor structure like most Gastropoda (Yamamoto 1985, Muntz and Wentworth 1987, Messenger 1991). The free head and other synapomorphic characters in cephalopods and gastropods (Salvini-Plawen 1990, Salvini-Plawen and Steiner 1996, Haszprunar 2000) suggest the cerebral eyes of both groups (= Visceroconcha) as being homologous although evolved to different complexity. *Nautilus* Linnaeus, 1758, exhibits simple pin-hole organs, whereas the Coleoida possess highly differentiated lens-eyes. Additional photoreceptors are the so-called photosensitive vesicles, viz. the epistellar bodies in Octobrachia and the parolfactory vesicles in Decabrachia (Salvini-Plawen and Mayr 1977, Messenger 1991, Cobb and Williamson 1998, Parry 2000). These "extraocular/ectoptic/extraretinal" organs are provided with microvillous receptor cells, contain the visual pigment rhodopsin, and show a depolarizing reaction to light.

Bivalvia

In Bivalvia, six different lines of photoreceptive organs may be recognized (Salvini-Plawen and Mayr 1977, Morton 2001; Fig. 2). One of these (1) includes cerebral ocelli, whereas five lines (2)-(6) are "extraocular/ectoptic/extraretinal" photoreceptors that originate at the mantle rim(s). The border of the mantle, including the siphons, appears to have acquired a general light sensitivity (see "dermal" light sense, above; Kennedy 1960, Mpitsos 1973, Morton 2001). This gave rise, at different mantle folds and in various groups (Morton 2001; see Fig. 2), to photoreceptive organs, all innervated by pallial nerves from the visceral ganglia.

(1) The cerebrally innervated, cup-like ocelli at the first branchial filament represent the larval ocelli (see above). In *Striarca lactea* (Linnaeus, 1758) they are located at the posterior labial palp (Thiele 1902: 380 and figs. 145-146). These organs persist for various times also in the adult animals. They occur in representatives of several pteriomorph families (Pelseneer 1908, Rosen *et al.* 1978, Morton 2001) and some may be provided with a simple lens (Morton 1978).

(2) A type of compound eye originates at the mantle edge of arcoidan representatives (cf. Morton 2001). This includes Arcidae, Glycimeridae (*Pectunculus* in Land 1984 = *Glycimeris* Da Costa, 1778), Cucullaeidae (*Cucullaea* Lamarck, 1801), and Limopsidae (*Philobrya* Carpenter, 1872). Such eyes parallel the compound ocelli of sabellid polychaetes as well as the complex eyes of arthropods (cf. Nilsson 1994, Land and Nilsson 2006). Each "ommatidium" lacks a real lens and represents an unusually modified ciliary photoreceptive cell accompanied by a supporting pigment cell (Levi and Levi 1971, Nilsson 1994). Each sensory cell is covered by a lateral expansion with microvillosities of the supporting cell and shows an inversed polarity: the nucleus is positioned distally and the median membrane enlargements of the laterally located cilia are arranged above each other in the basal third of the cell. They react to a decrease in light intensity.

(3) In Pteriomorpha, there are additional photoreceptive organs at the mantle edge (see Fig. 2) which may co-exist with compound eyes or even cerebral ocelli; this underlines that this clade as adapted to the eulittoral zone. They show a wide morphological range in configuration and structure. Examples include the simple cap-shaped eyespots in Pteri-

oidea (*e.g., Isognomon* Lightfoot, 1786; Morton 2001), simple everse pigment-cup pits in Arcoidea (*e.g., Arca* Linnaeus, 1758; Nilsson 1994), pinhole-like organs in Limoidea (*e.g., Lima* Bruguière, 1797; Hesse 1900 and below), everse lens eyes in Limoidea (*e.g., Ctenoides* Mörch, 1853; Morton 2001) as well as on the outer surface of the mantle in Anomioidea (*e.g., Enigmonia* Iredale, 1918; Morton 2001), and the unusual organs with lens and two retinae in Pectinoidea (Pectinidae, Spondylidae).

With respect to the receptor structure among Pteriomorpha, except for Pectinoidea, only the pigment-cup photoreceptive organs in Arcidae have been investigated (*Arca, Barbatia* Gray, 1842, *Anadara* Gray, 1847; Nilsson 1994). More ultrastructural studies in other Pteriomorpha are needed. The organs of Arcidae are rhabdomeric. In the study by Steiner (2001), three additional species were ultrastructurally investigated: the two pectinids *Chlamys varia* (Linnaeus, 1758) and *Pseudamussium peslutre* (Linnaeus, 1771) as well as the limoidean *Lima lima* (Linnaeus, 1758) [= *Lima squamosa* Lamarck, 1891]. The eye structure of the two pectinids (Fig. 3) is similar to that of *Pecten maximus* (Linnaeus, 1758) (see Barber *et al.* 1967), *i.e.*, an inverted retina of rhabdomeric receptors as well as a distal retina of everse ciliary receptor cells. The organs possibly function as concave mirror eyes (Land 2000). In both species, the upper, everted retina shows cells with distally flattened cilia arranged in whorls (Fig. 4A). Central microtubules and rootlets are lacking. The two species differ from *Pecten* in that the proximal rhabdomeric receptor cells have numerous long ciliary rootlets (Figs. 4B, 5). The cornea cells are also considerably taller at the center than peripherally (see also Morton 2001 for *Patinopecten yessoensis* (Jay, 1857) and *Chlamys pusio* (Linnaeus, 1758)). Another major difference is in the arrangement of the proximal retina. Whereas in *Chlamys varia* the rhabdomeric receptive regions of the long sensory cells form a closed layer below the distal retina, their nucleus-containing regions are fairly peripherally arranged. In contrast, the proximal retina of *Pseudamussium peslutre* does not form a continuous layer below the distal retina; rather, the ciliary retina, which is smaller in diameter, is only peripherally underlain by the rhabdomeric receptive regions (Fig. 3). Thus, the proximal retina in *Pseudamussium* merely forms an incomplete, ring-like layer centrally without receptors. In the eye axis, only the distal, ciliary retina probably functions for photoreception.

The distally open photoreceptive organs of *Lima lima,* without cornea or lens, are formations of the periostracal groove between outer and middle mantle folds (Fig. 6). As already roughly described by Mpitsos (1973) for *Lima scabra* (Born, 1778), rhabdomeric and ciliary sections are separable in the retina; Nasi (1991) figured isolated rhabdomeric sensory cells with a distal microvillous lobe. Similarly, the retina

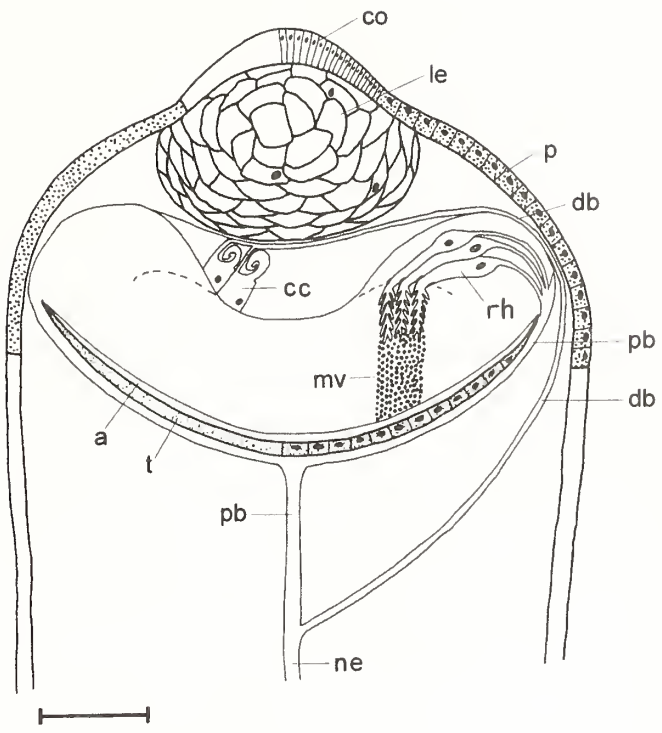

Figure 3. *Pseudamussium peslutre* (Bivalvia). Diagram of a longitudinal section of the eye. a, argentea; cc, ciliary retina cell; co, cornea; db, distal branch of optic nerve; le, lens; ne, optic nerve; p, epidermal pigment ring; pb, proximal branch of optic nerve; rh, rhabdomeric sensory cell; t, pigmented tapetum cells. The transition from the cell bodies (proximal retina) to the rhabdomeric rod is marked by desmosomes (dotted line). Scale bar = 100 μm. (From Steiner 2001).

of *L. lima* is divided into two regions, the proximal rhabdomeric and pigmented cells on the one hand, and distal ciliary receptor cells on the other hand. The latter also show some microvilli. In *L. lima*, however, the transition from rhabdomeric to ciliary receptors is gradual. The rhabdomeric cells show several cilia at the "neck" leading to the bulbous receptive portion (Fig. 7), thus perhaps representing a mixed type. The ciliary receptors lack rootlets as well as central microtubules, and the vast enlargements of their ciliary membrane surfaces fill the eye cavity ("vitreous mass", Fig. 8; compare *Tridacna* Bruguière, 1797, below). Part of the middle mantle fold, above the periostracum-secreting cells, shows cells with large void spaces and few organelles, thus representing a "window" for the light (Fig. 6).

No decision can be made as to a homology versus a homoiology of all these photoreceptive organs at different mantle folds between the pteriomorph family groups (see also Morton 2001, 2008). Particularly, no known configuration of photoreceptive organ forms a transition to the ex-

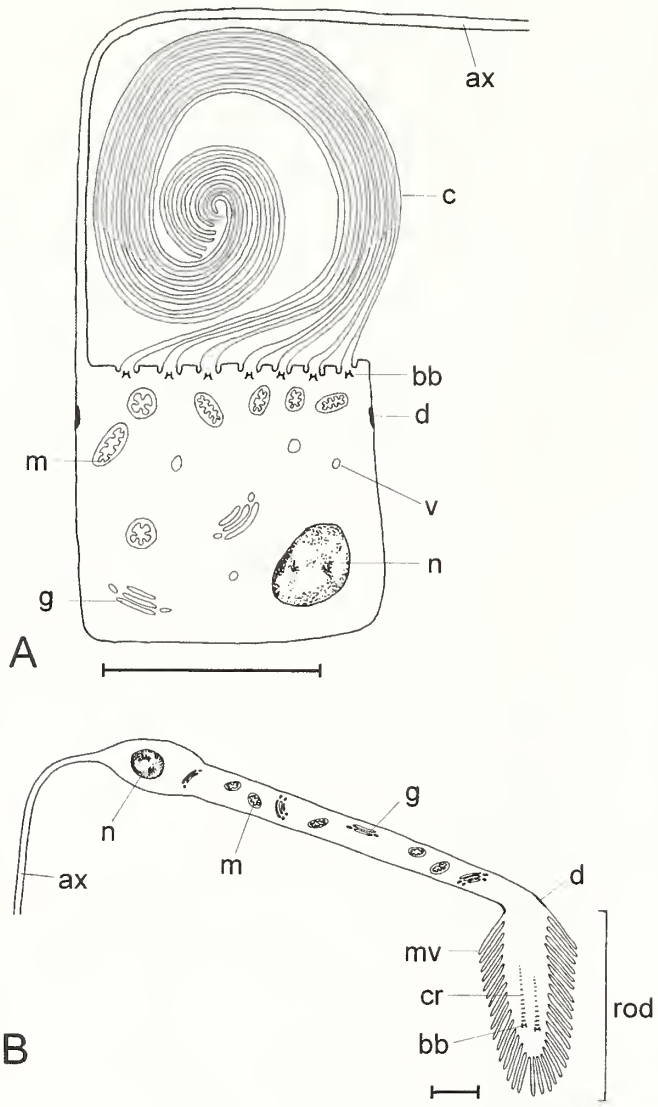

Figure 4. *Chlamys varia* (Bivalvia). A, Ciliary sensory cell of the distal retina. Scale bar = 5 μm. B, Rhabdomeric sensory cell of the proximal retina. Scale bar = 10 μm. a, axon; bb, basal body; c, cilia; cr, ciliary rootlet; d, desmosomes; g, Golgi stack; m, mitochondrion; mv, microvilli; n, nucleus; v, vesicle. (From Steiner 2001).

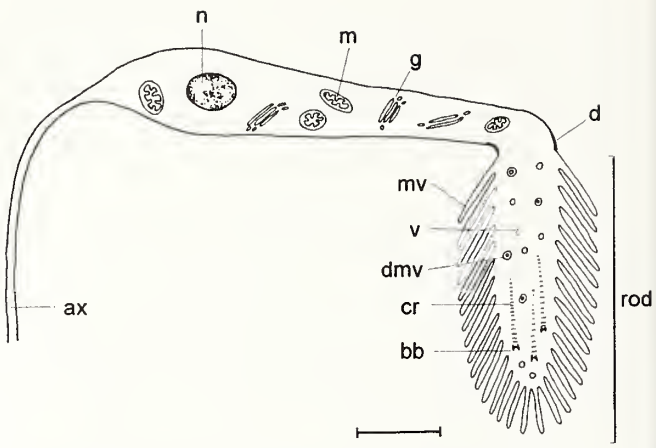

Figure 5. *Pseudamussium peslutre* (Bivalvia). Rhabdomeric sensory cell of the proximal retina. ax, axon; bb, basal body; cr, ciliary rootlet; d, desmosome; dmv, double-membraned vesicle; g, Golgi stack; m, mitochondrion; mv, microvilli; n, nucleus; v, vesicle. Scale bar = 10 μm. (From Steiner 2001).

traordinary eyes of Pectinoidea. The earlier reference (Salvini-Plawen and Mayr 1977, Salvini-Plawen 1982) to a morphological sequence has been questioned (Morton 2001), *i.e.*, that an "accessory receptor" of inverse eyes (such as in Cardiidae, below) could have been modified to the distal retina in Pectinoidea. The very distant relationship of the representatives (Veneroidea versus Pteriomorpha; see Fig. 2) and the independent formation of two retinae in *Laternula* Roeding, 1798 (Anomalodesmata, below) renders the hypothesis speculative. The existence of an "accessory organ" associated with the photoreceptors also in some Pteriomorpha (*e.g.*, *Philobrya* Carpenter, 1872, *Enigmonia*; see Morton 2001), however, does not exclude such a structural sequence as a differentiation model for the eyes of Pectinoidea. An alternative view (see also Steiner 2001) refers to the more closely related Limoidea (see Fig. 2), whose retina shows two sections. A major shift and concentration of their ciliary cells (distal section) towards the light-exposed side, followed by their separation and medial inversion, would form a primordial distal retina. This would be followed by later reversion to everse cells (compare organogenesis in pectinids; Hesse 1908, Küpfer 1916). In the proximal section, a concentration of the pigment cells mid-ventrally (eventually becoming a tapetum) and separation from the lateral (rhabdomeric) receptive cells would favor a medially directed inversion of the latter. This would then represent a peripheral proximal retina such as in *Pseudamussium peslutre*.

(4) Within Anomalodesmata-Pandoroidea-Pandoridae, the unusual pallial photoreceptive organs in *Laternula* species [= *Anatina* in Pelseneer 1908, footnote] are situated on tentacles around the siphons. The eyes with lens have two retinae above each other, both built up (in contrast to Pectinoidea) of everse cells with ciliary receptor structure. They are surrounded by a cup of pigment cells delimited by a sclerotic coat (Adal and Morton 1973). Similar to the accessory receptors in Cardiinae and Tridacninae, an eye appendage associated with the optic nerve is present; this includes a vertical channel with a bundle of long cilia at its base and apparently represents a mechanoreceptor (Morton 2001).

Other photoreceptive organs are reported in Pandoroi-

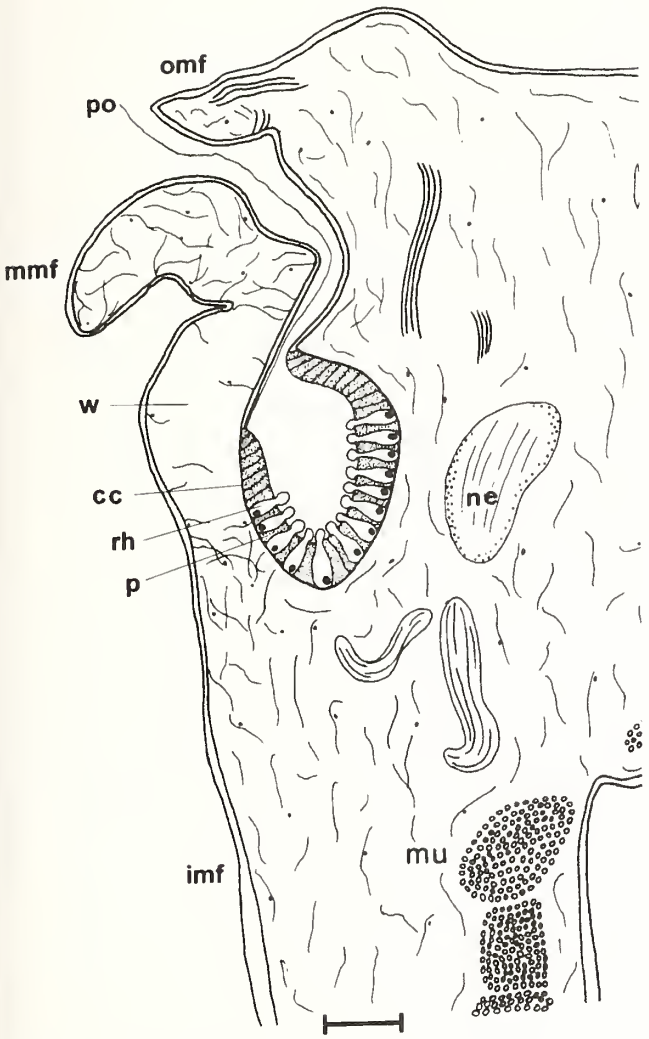

Figure 6. *Lima lima* (Bivalvia). Diagram of a longitudinal section of the mantle folds with the eye cup. cc, ciliary sensory cells; imf, inner mantle fold; mmf, middle mantle fold; mu, muscle; ne, nerve; omf, outer mantle fold; p, pigment cell; po, periostracum; rh, rhabdomeric sensory cell; w, "window". Scale bar = 100 μm. (From Steiner 2001).

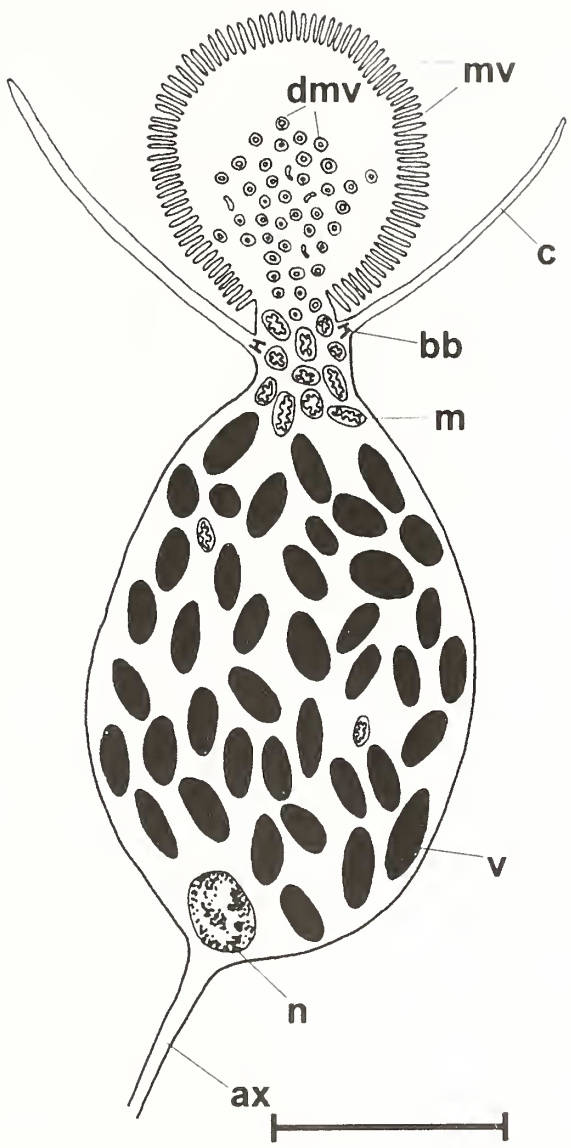

Figure 7. *Lima lima* (Bivalvia). Diagram of a rhabdomeric sensory cell of the proximal eye cup. bb, basal body of cilium, c, cilium; dmv, double-membraned vesicle; m, mitochondrion; mv, microvilli; n, nucleus; v, vesicles. Scale bar = 20 μm (from Steiner 2001).

dea-Lyonsiidae by Prezant (1984) for *Lyonsia hyalina* (Conrad, 1831) along the exhalant siphon. These lens-eyes have pigment cells and they have ciliary sensory cells with the membrane-enlargements in whorls. Proximally, these whorls form concentric rings similar to those in *Laternula* (above).

(5) Among Veneroida, members of the more closely related Cardiinae and Tridacninae (Cardioidea) show photoreceptive organs at the siphonal tissues; in Cardiinae a large number is present at the tips of tentacles. In *Cerastoderma edule* (Linnaeus, 1758) the eyes are more or less inverted without a lens and the receptor cells (ciliary type) are enclosed in a cup of reflecting cells (Barber and Wright 1969). The inner epithelium of the tentacle, basal to the eye cup, contains pigment granules that presumably also serve as a reflecting surface (Morton 2001). In addition, an "accessory receptor organ" at the tip of the tentacle is associated with the optic nerve. Its receptor cells bear numerous unmodified cilia and microvilli.

In *Tridacna*, the abundant eyes are everse and the receptor cells are of the ciliary type. The mass of the microvillous membrane-enlargements of the cilia may also function as a lens ("vitreous mass"; see *Lima*, above). No cup of

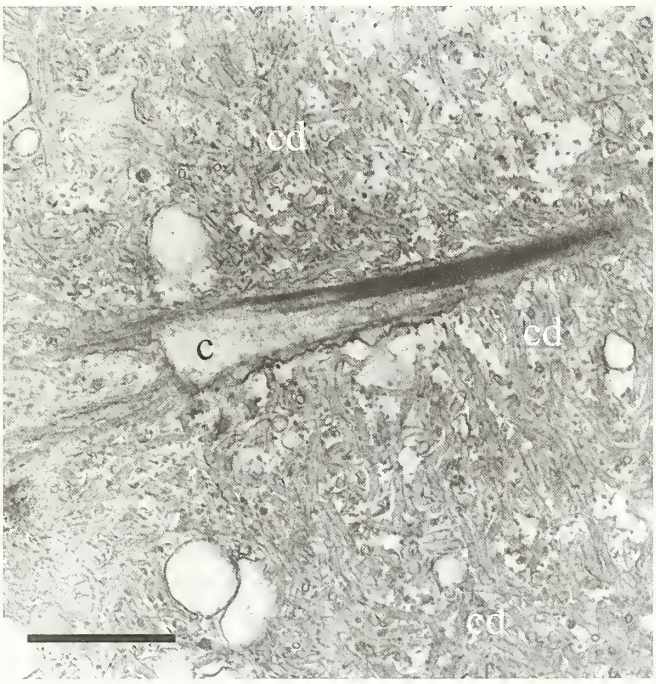

Figure 8. *Lima lima* (Bivalvia). Ultrastructural section of a ciliary sensory cell of the distal area of the retina with tube-like diverticles of the ciliary membrane filling the eye cup ("vitreous mass"). c, cilium; cd, tube-like diverticles. Scale bar = 1 μm. (From Steiner 2001).

pigment cells is present, but surrounding layers of olive-green zooxanthellae may have a reflective function (Frankboner 1981). A ciliated "accessory receptor" is associated with the optic nerve.

(6) Within Myoida, thousands of pear-shaped, pigment-less cells have been reported and described in the siphons of *Mya arenaria* Linnaeus, 1758 (Light 1930). They are differentiated just beneath the inner epithelium of both (incurrent and excurrent) siphons. No fine structural investigation is available, but these cells, which have axons to the siphonal nerves and an enclosed optic organelle, are devoid of associated shading pigment. They nonetheless react to an increase in light intensity with contraction of the joined siphons. These pear-shaped cells thus parallel the phaosome cells in Clitellata in both structure and function (see Purschke 2003), the latter representing unicellular photoreceptors.

FINAL CONCLUSION

The proposed evolution of photoreceptors according to two different, successive processes is compatible with the general expression of transcription factor genes as well as with the rich morphological diversity of the photoreceptive organs throughout the metazoans. Earlier representations with respect to this polyphyly are now modified: the structural types of the epidermal photosensitive receptors (ciliary, rhabdomeric) are now considered to be mere morphs, obviating the need for arguments on homology or non-homology. The homology identification of photoreceptors must, therefore, follow other precise criteria (relationship, continuity, structural and/or developmental intermediates, identical gene regulatory network). According to such criteria, evolutionarily independent structural differentiation (morphogenesis) of photoreceptors in Mollusca can be proposed for at least thirteen lines (Table 1), irrespective of potential multiple homoiology of pallial organs within pteriomorph Bivalvia (Fig. 2).

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